

THE STEMS OF CLIMBING PLANTS.

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(Plates lx.-lxvi.).

In botanical excursions with the Field Naturalists' Club or Royal Society, it has been a constant source of interest that climbing plants of the Orders Bignoniaceæ and Menispermaceæ could be partly determined by studying the cut ends of their stems. This determination extended only to the Order, and not to the genus or species. In Bignoniaceæ, the determining factor was the arrangement of the bast in four masses, or in multiples of four, each mass usually presenting rectangular outlines in transverse section. In Menispermaceæ, the rays of wood and bast have usually a stellate arrangement, the vascular bundles being separated by broad, multiseriate medullary rays, which, in transverse sections of the stem, appear club-shaped from dilation of the last-formed cells.

To test whether similar peculiarities marked the structure of climbing plants of other Orders, some fifty-three stems were sectioned, and their slides photographed by my colleague, Mr. C. A. Lambert.

List of Species examined.

ACANTHACEÆ.—*Thunbergia grandiflora* Roxb., *T. laurifolia* Lindl.

AMPELIDEÆ.—*Vitis hypoglauca* F.v.M., *V. opaca* F.v.M., *V. sterculiifolia* F.v.M.

APOCYNACEÆ.—*Beaumontia grandiflora* Wall., *Melodinus acutiflorus* F.v.M., *Trachelospermum jasminoides* Lindl.

ASCLEPEDIACEÆ.—*Cryptostegia grandiflora* R.Br.

BIGNONIACEÆ.—*Adenocalymma nitidum* Mart., *Bignonia floribunda* H.B. & K., *B. picta* Lindl., *B. Tweediana* Lindl., *B. venusta* Ker, *Tecoma Hillii* F.v.M., *T. jasminoides* Lindl.

COMBRETACEÆ.—*Quisqualis indica* Roxb.

COMPOSITÆ.—*Senecio tamoides* DC.

CONVOLVULACEÆ.—*Ipomœa Horsfalliæ* Hook.

CUCURBITACEÆ.—*Bryonia laciniata* Linn.

LEGUMINOSÆ.—*Abrus precatorius* Linn., *Bauhinia scandens* Burm., (= *B. corymbosa* Roxb.), *Derris scandens* Benth., *Lathyrus odoratus* Linn., *Milletia australis* F.v.M., *M. megasperma* F.v.M., *Wistaria chinensis* DC.

LOGANIACEÆ.—*Buddleia madagascariensis* Vahl.

MALPIGHIACEÆ.—*Banisteria chrysophylla* Linn., *Hiptage Madablota* Gærtn., *Stigmaphyllon jatrophaefolium* Juss.

MENISPERMACEÆ.—*Carronia multiseptata* F.v.M., *Legnephora Moorii* Miers, *Stephania hernandicefolia* Walp.

NYCTAGINEÆ.—*Bougainvillea lateritia* Hort., *B. Sanderiana* v. *variegata* Hort., *B. spectabilis* Juss.

PASSIFLOREÆ.—*Passiflora suberosa* Linn.

PIPERACEÆ.—*Piper nigrum* Linn.

POLYGONACEÆ.—*Antigonon leptopus* Hook.

RUBIACEÆ.—*Celospermum paniculatum* F.v.M.

SOLANACEÆ.—*Solanum Wendlandii* Hook. f.

URTICACEÆ.—*Ficus pumila* Linn.

VERBENACEÆ.—*Faradaya splendida* F.v.M., *Petrœa volubilis* Linn.

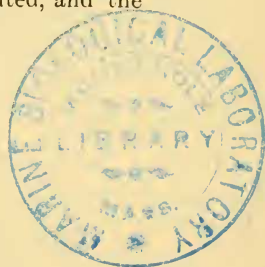
AROIDEÆ.—*Monstera acuminata* C. Koch, *Pothos aureus* Linden.

FLAGELLARIEÆ.—*Flagellaria indica* Linn.

LILIACEÆ.—*Asparagus racemosus* Willd., *Geitonoplesium cymosum* A. Cunn., *Rhipogonum album* R.Br., *Smilax australis* R.Br.

ORCHIDACEÆ.—*Galeola cassythoides* Reichb.

The study had not proceeded far, when it was seen that any grouping in Natural Orders was impossible, as similar characteristics were common to plants of many different families, especially among Dicotylédons. It was necessary, therefore, to create classes, among which the stems could be distributed, and the following are submitted.



Subclass i. DICOTYLEDONES.

1. **Normales**.—The stem shows a single cambium-ring, with the wood and bast of each bundle lying along the same radius, the exterior outline of the bast approximating to a circle. Type, *Cælospermum paniculatum* F.v.M.

2. **Chiastoxylon**.—A single zone of cambium, with anomalous distribution of tissues in young stems into four rays, each of alternating wood and bast, the bast reaching (a) partly to the pith, or (b) stopping short of it. Type 2 (a), *Bignonia Tweediana* Lindl., 2 (b), *B. picta* Lindl.

3. **Astroxylon**.—Normal cambium, with definite and continuous separation of fibro-vascular bundles by means of pluriseriate medullary rays, that present, in transverse section, a stellate arrangement. Type, *Carronia multisepalea* F.v.M.

4. **Endophloia**.—Besides the normal bast, a second development of bast occurs at the inner margin of the ring of wood, forming bicollateral bundles. Type, *Bryonia laciniosa* Linn.

5. **Exocycla**.—Besides the normal cambium-ring, new cambium-zones appear successively in centrifugal order. Type, *Wistaria chinensis* DC.

6. **Phloiocycla**.—New zones of bast produced in each period of vegetation in centripetal order. Type, *Vitis sterculiifolia* F.v.M.

7. **Polycycla**.—The oldest vascular bundles lie in the pith; outside the pith, a normal zone of wood and bast is formed, or alternating rings of wood and bast may be formed. Type, *Bougainvillea spectabilis* Hort.

Subclass ii. MONOCOTYLEDONES.

1. **Vulgares**.—Possessing the usual rind, hard ground-parenchyma, and scattered, closed bundles of the ordinary monocotyledon.

2. **Abnormales**.—Differing from the typical monocotyledonous stem in one or other of the above peculiarities.

Subclass i. DICOTYLEDONES.

1. **Normales**.—To this section belong *Banisteria chrysophylla* L., *Cælospermum paniculatum* F.v.M., *Cryptostegia grandiflora* R.Br., *Faradaya splendida* F.v.M., *Hiptage Madablota* Gærtn.,

Milletia australis F.v.M., *M. megasperma* F.v.M., *Senecio tamoides* DC., *Solanum Wendlandii* Hook. f., and *Tecoma jasminoides* Lindl., etc., etc.

(a.) CŒLOSPERMUM PANICULATUM F.v.M. (Plate lx., fig.1).—Although this stem is normal in having a single ring of cambium, and in regard to the formation of secondary wood, the pith presents peculiarities. It is made up of two elements; one, the ordinary pith-cell, containing starch; and the other, found mainly in the centre of the pith, a thick-walled, sclerotic cell. The latter form strands which do not extend to the circumference of the pith. They are akin to the gum-resin sacs, described by Karsten,* in the allied genera, *Cinchona* and *Ladenbergia*.

(b.) MILLETIA AUSTRALIS F.v.M. (Plate lx., fig.2).—Although normal in the development of its cambium-ring, this stem shows some special features. The pith is of very large cells, and, in transverse section, these seem to be radially arranged, forming conical masses. In the rays, the cells are elongated, and have not the usual hexagonal outline. The cambium-ring is very well defined, and, outside the bast, is a sclerenchymatous ring, 6 to 8 cells in depth, with intervals in which are inserted a few, much larger, thinner-walled cells, evidently a transfusion-tissue. Sacs containing single crystals abound in the cortex, and others with much larger single crystals are scattered through the pith.

MILLETIA MEGASPERMA F.v.M.—The arrangement of the pith is normal. The wood-vessels form radial rows, with large masses of murally arranged wood-fibres between them. There is a thick sclerenchymatous ring outside the bast, with transfusion-tissue at intervals; but, in this species, the thin-walled cells are oval, and elongated along radii passing through the transfusion-tissue. A second, much narrower, sclerenchymatous ring separates the periderm from the cork. The medullary rays differ little, in a transverse section from the wood-parenchyma.

(c.) SOLANUM WENDLANDII Hook. f., (Plate lxi., fig.3).—The central pith is of large cells. The ring of wood is very regular, the wood-fibres showing very even ranks, the cells increasing in size towards their inner boundary, and gradually merging in

* Karsten, Die medic. China-rinden Neu-Grenadas, Ges. Beitr., p.382.

those of the pith. Outside the bast is a ring of sclerenchymatous cells, that apparently acts as an endodermis also. The bark shows all the usual tissues excellently—phelloderm, phellogen, cork, and epidermis with cutin. Scattered, sclerenchymatous elements are found also in the circumferential parts of the pith.

2. *Chiastoxylon*.

(*a.*) *BIGNONIA TWEEDIANA* Lindl., (Plate lxi., fig 4).—In transverse section, the pith is roughly square in outline, and a rectangular ray of bast strikes the centre of each side of the square at right angles or nearly so. From the inner end of each bast ray, a small cone of wood (protoxylem) penetrates the pith to about one-sixth of its diameter. The pith-cells are filled with starch-grains. The wood is continuous round the pith, but forms a very narrow connecting band at the base of each bast-ray, near the protoxylem-masses already mentioned. The vessels occur in V-shaped bands, which are most definite near the bast. The wood-parenchyma forms irregular, radiate rows. The bast-rays project into the cortex at their circumferential limit, and preserve their shape as rectangular masses. Their bast consists of alternating strips of hard and soft bast, the latter of more rows of elements. The bast-rays are connected by a bast-ring surrounding the four masses of wood, and showing alternate strips of hard and soft bast, as in the rays. There is an incomplete circle of sclerenchyma within the phellogen, beyond which are 6-7 tiers of cork-cells bounded by dead bark.

(*b.*) *BIGNONIA PICTA* Lindl., (Plate lxii., fig. 5).—The bast forms four square masses of five thin layers of hard bast, alternating with five broader layers of soft bast. Where these masses occur, the wood-tissues have about half their usual depth, and press on the central pith, giving it almost a square outline. The cambium is thick and definite. It is depressed at each of the bast-patches, so that the cambium-ring has a crenulated outline. On a circle outside the bast are a number of roughly elliptical masses of thick-walled sclerenchyma. A second narrow and almost complete ring of sclerenchyma, bounding the cork-cambium, is constructed of brick-shaped cells, whose cavities are almost obliterated.

3. **Astroxylon**.—Type, *CARRONIA MULTISEPALEA* F.v.M., (Plate lxii., fig.6).—The stele consists of a central pith, composed of very fine polygonal cells in which a few thick-walled ducts are inserted at irregular intervals. Of wood and bast, there are about thirty fibro-vascular bundles, each showing six to eight large vessels, increasing in size, as usual, from the centre outwards. Bordering the pith in each, is a cluster of mainly spiral vessels. Each medullary ray is well defined, and shows five to eight rows of brick-shaped cells, parting at the circumferential end to send, right and left, divisions round the separated bundles. The bast-masses are oval and well defined. They are flanked outwardly by older bast-tissues, now changed into sclerenchyma, to be finally cast off with the outer bark. The different layers of the bark are well defined, and the phelloderm assumes a wavy outline, parallel to the outward curves of the various bundles.

Lighter in colour than the rest of the stele, the medullary rays present a stellate pattern on a freshly cut, transverse section of the stem.

4. **Endophloia**.—*BRYONIA LACINIOSA* Linn., (Plate lxiii., fig.7).—The development of the stem is apparently normal, but the vascular bundles are bicollateral, having bast on both inner and outer faces. The vessels of the xylem are unusually large for a young stem in its second year of development. A large pad of cork is seen on the side of the stem that has flattened by pressure against the supporting plant. Very little pith is to be noted, and the cells of the medullary rays are peculiarly large and broad. There are signs of the production of interfascicular bast from the sides of vascular bundles.

5. **Exocycla**.—*WISTARIA CHINENSIS* DC., (Plate lxiii., fig.8).—The medullary rays are exceedingly well defined, usually of 2-6 rows of radially elongated cells. At their outer extremities, the cells, lying in the bast, are of larger size. The cambium-ring is also clearly defined, and outside it are 6-8 ranks of thin-walled bast-cells. The older bast-cells, pushed out towards the circumference, have most of their cavities obliterated by internal thickenings. The phellogen-ring is also well marked, and 3-5 layers of dead cells lie outside the cork. Cortex and pith show sacs

containing single, lozenge-shaped, octahedral crystals. The remains of a former cambium-ring are seen in the wood about one-third of the distance from pith to cortex. A third cambium-ring is seen forming in the bast, from which additional rings of xylem and phloëm will be created.

6. *Phloiocycla*.—*VITIS STERCULIFOLIA* F.v.M., (Plate lxiv., fig. 9).—The pith appears homogeneous. The medullary rays, 2-8 rows of radially arranged, brick-like cells, contrast clearly with the murally arranged wood-fibres. The vessels are large, and evidently capable of division. The medullary rays are as well defined between the bast-masses as between the wedges of wood. They increase in size towards the circumference of the transverse section, and take a clavate outline. The bast is composed of 8-10 rows of thin-walled cells, with a terminal, almost circular mass of sieve-tubes. Outside the stele, the remains of former bast-masses, now sclerotic, form a strengthening layer in the cortex. A few sacs containing raphides may be noted here and there; others contain single, larger, flattened crystals, and others, again, store starch-grains.

7. *Polycycla*.

(a.) *BOUGAINVILLEA SPECTABILIS* JUSS., (Pl. lxiv., fig. 10).—The centre of the transverse section of the stem contains the largest vascular bundles, scattered through the pith. The xylem and phloëm portions of each bundle are clearly defined, but the cambium is usually marked by a scar, where it has torn under the knife of the microtome. Outside these older and scattered bundles, is a clearly defined ring of two years' growth of younger bundles, normally dicotyledonous in general appearance, but having alternate circles of wood, bast, wood, bast. Between any two bundles of the outer ring are well defined medullary rays; but, at the interior end of each ray, the cells composing it become roughly polygonal, and merge into the pith-cells. When a new cambium appears, outside the last ring of bundles, the cells of the outer ends of the rays unite round the outer extremity of each bundle, so as to isolate the ring previously formed by a definite wavy circle of parenchymatous tissue. The bast arising

from this latest-formed cambium consists of 6-8 rows of brick-like, thin-walled cells, outside of which is a single-rowed circle of sclerenchyma.

(b.) *BOUGAINVILLEA LATERITIA* Hort., (Plate lxx., fig.11), differs little from *B. spectabilis* and *B. Sanderiana*, except that numerous sacs containing clinorhombic crystals—raphides—are found in the periderm and pith. Where a bud is formed on the stem, the tissues entering the bud from the stele are full of these needle-crystal sacs.

(c.) *BOUGAINVILLEA SANDERIANA* Hort., (Plate lxx., fig.12).—This section ($\times 90$) shows the central and first-formed vascular bundles isolated in the pith, as in the case of its allies; and four annual zones of alternating wood, bast, and encircling medullary ray-tissue. This last might be taken for cambium, but is quite distinct in the character of the cells composing it, from that of the last-formed cambium-ring. Periderm, cork, and the dead cells of the outer bark are well shown.

(d.) *PIPER NIGRUM* Linn., (Pl. lxxi., fig.13).—The general structure of this stem is similar to that of *Bougainvillea*. The first-formed set of bundles, seven in number, develops cambium within each bundle, but not between them. These bundles are further isolated by the growth of the pith. Circumferentially, other cambium-tissues form, making a complete wavy ring, and give rise to a normally developed set of vascular bundles of the usual dicotyledonous arrangement. Lying in the pith, outside each of the original isolated bundles, is a resin-duct; and a larger one occupies the centre of the stem. Bounding the outer, normal ring of vascular bundles on the inner side, is a complete wavy ring of sclerenchyma, of about six irregular rows of thickly strengthened, polygonal cells. An indefinite ring of sclerenchyma, its cells elongated circumferentially, surrounds the outer ring of wood and bast.

STEPHANIA HERNANDIÆFOLIA Walp.—In a first year's shoot, there is a remarkable similarity between the cells of the pith, medullary rays, and periderm. As in *Piper nigrum*, the stele is bounded by a scalloped line, outside of which new cambiums arise, and new rings of wood and bast are developed.

ii. MONOCOTYLEDONES.

1. **Vulgares.**—To this section belong *Asparagus racemosus* Willd., *Flagellaria indica* Linn., *Geitonoplesium cymosum* A. Cunn., *Rhipogonum album* R.Br., and *Smilax australis* R.Br., &c.

2. **Abnormales.**—*GALEOLA CASSYTHOIDES* Reichb. f., (Pl. lxvi., fig.14).—In this leafless, climbing orchid, the bundles are numerous, and contain six large vessels, with a few smaller marking the protoxylem. In each vascular bundle there is a limited quantity of soft bast, and a few sieve-tubes. The ground-parenchyma is formed of larger cells than usual, and these are massed round the bundles, forming bundle-sheaths. In transverse sections of the stem, a roughly radiate arrangement of the cells of the ground-parenchyma is evident, in some sections showing four rays, in others with more and irregular rays. Numerous sacs containing raphides are seen in the ground-tissue. The contents of cells lying immediately within the bark show a brown discoloration; these are evidently attacked by a parasitic fungus, whose hyphæ can be seen within the brown cells.

Conclusion.—The whole of the abnormal stem-structures in climbing plants have, for their object, the free flow of elaborated sap in the bast-tissues. In *Chiastoxylon*, the stem so presses on the support as not to put pressure on the bast-masses; in *Astroxylon*, the broad medullary rays ensure the nutrition of the stele; in *Hiptage*, *Bryonia*, and *Solanum Wendlandii*, a thick pad of elastic cork is developed on that side of the stem subject to pressure, and so on.

Reference letters.—*b.*, Bast—*c.*, Cambium—*c.c.*, Cork-cambium—*ck.*, Cork—*cr.*, A crystal—*ew.*, Protoxylem—*fb.*, Fibro-vascular bundle—*h.*, Hair—*m.r.*, Medullary ray—*p.*, Pith—*ph.*, Phelloderm—*r.d.*, Resin-duct—*ry.*, (Fig.14), Three of the four rays traversing the ground-parenchyma—*s.*, Sclerotic cells—*sc.*, Sclerenchyma—*s.v.b.* (Fig.14), Secondary vascular bundles—*t.t.*, Transfusion-tissue—*v.*, Vessels of wood—*v.b.* (Fig.14), Vascular bundle with apparent bundle-sheath—*w.*, Wood— \times (Fig.14), Traces of fungal hyphæ.

EXPLANATION OF PLATES LX.-LXVI.

Plate lx.

Fig.1.—T.S. *Carlospermum paniculatum* F.v.M.; ($\times 24$). [1. **Normales**].

Fig.2.—T.S. *Milletia australis* F.v.M.; ($\times 17$). [1. **Normales**].

Plate lxi.

Fig.3.—T.S. *Solanum Wentlandii* Hook. f.; ($\times 90$). [1. **Normales**].

Fig.4.—T.S. *Bignonia Treediana* Lindl.; ($\times 17$). [2 **Chiastoxylon**].

Plate lxii.

Fig.5.—T.S. *Bignonia picta* Lindl.; ($\times 23$). [2. **Chiastoxylon**].

Fig.6.—T.S. *Curronia multispalea* F.v.M.; ($\times 13$). [3. **Astroxylon**].

Plate lxiii.

Fig.7.—T.S. *Bryonia luciniosa* Linn.; *ck.*, cork-layers on side facing support; ($\times 23$). [4. **Endophloia**].

Fig.8.—T.S. *Wistaria chinensis* DC.; ($\times 40$). [5. **Exocycla**].

Plate lxiv.

Fig.9.—T.S. *Vitis sterculiifolia* F.v.M.; ($\times 40$). [6. **Phloiocycla**].

Fig.10.—T.S. *Bougainvillea spectabilis* Juss.; *ck.*, pad of cork opposite supporting branch; ($\times 23$). [7. **Polycycla**].

Plate lxv.

Fig.11.—T.S. *Bougainvillea lateritia* Hort.; ($\times 90$). [7. **Polycycla**].

Fig.12.—T.S. *B. Sanderiana* v. *variegata* Hort.; ($\times 90$). [7. **Polycycla**].

Plate lxvi.

Fig.13.—T.S. *Piper nigrum* Linn.; ($\times 40$). [7. **Polycycla**].

Fig.14.—T.S. *Galeola cassythoides* Reichb.; ($\times 19$). [MONOCOTYLEDON: 2. **Abnormales**].